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The stereoscopic (cyclopean) motion aftereffect is selective for spatial frequency and orientation of disparity modulation

Stephanie Shorter, Christopher Bowd, Michael Donnelly, Robert Patterson *

Department of Psychology, Program in Neuroscience, Washington State University, Pullman, WA 99164-4820, USA

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Abstract

Across two experiments, this study investigated the spatial frequency tuning and orientation tuning (both in the disparity domain) of the stereoscopic (cyclopean) motion aftereffect. In Experiment 1, observers adapted to a moving stereoscopic grating of a given cyclopean spatial frequency and tested for the motion aftereffect with a static grating of the same or different spatial frequency. Robust motion aftereffects were induced only when the spatial frequency of the adapt and test stimuli was the same. In Experiment 2, observers adapted to a moving stereoscopic grating of a given cyclopean orientation and tested for the motion aftereffect with a static grating of the same or different orientation. Robust motion aftereffects were induced only when the orientation of the adapt and test stimuli was the same. Together, these results suggest that the stereoscopic motion aftereffect is tuned for cyclopean spatial frequency and orientation which, in turn, suggest that the stereoscopic motion aftereffect is mediated by low-level oriented spatial-frequency mechanisms. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Motion processing in the human visual system exploits multiple sources of information. One source of information for motion processing is the movement of stimulus boundaries defined by differences in binocular disparity, called *stereoscopic motion* (Patterson, Ricker, McGary & Rose, 1992). Stereoscopic motion would arise, for example, when an observer binocularly views a target moving in front of a stationary background. The moving boundary created by the difference in depth between target and background would provide moving binocular disparity information to the motion system. Stereoscopic motion is processed subsequent to disparity at binocular-integration, or cyclopean (Julesz, 1971), levels of vision.

A controversy exists as to the kind of mechanism that computes stereoscopic motion. There are suggestions that stereoscopic motion is processed by a position-tracking mechanism. These suggestions come from studies that have found poor performance on tasks involving stereoscopic motion discrimination. For example, Lu and Sperling (1995a,b) investigated direction discrimination of a stereoscopic compound stimulus (i.e. corrugated surface in depth) that contained stereoscopic motion in the X/Y plane but no trackable features. These authors found that direction discrimination of the stereoscopic stimulus was poor, presumably because trackable features were absent. Lu and Sperling proposed that stereoscopic motion was processed by a feature tracking system that involved a motion energy analysis operating on the outputs of feature detectors.

In two studies, Harris and Watamaniuk (1995, 1996) examined speed discrimination of stereoscopic and luminance motion and found that speed discrimination was poor with stereoscopic motion compared with luminance motion. These authors suggested that stereoscopic motion was processed over a restricted range of spatio-temporal frequency that precluded precise speed discrimination, and that there was no specialized mechanism for processing the speed of stereoscopic motion. In a different study, Harris, McKee and Watamaniuk (1998) investigated detection of a single small luminance dot (target) moving in the Z-axis (which involved dynamic change in disparity) versus detection of a

* Corresponding author. Fax: +1-509-3355043.
E-mail address: rpatter@mail.wsu.edu (R. Patterson)

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single target dot moving in the X/Y plane (no dynamic change in disparity). In both cases, the target had to be detected as it moved through a group of stationary noise dots. These authors found that detection performance was good for motion in the X/Y plane, whereas performance was poor for motion in the Z-axis. They suggested that the target moving in the Z-axis was detected by a position-tracking mechanism (which presumably was why the stationary noise dots degraded performance for the Z-axis motion).

In some of these studies, failure to find evidence for good stereoscopic motion discrimination was likely due to the use of inappropriate stimulus parameters. Recall that Lu and Sperling (1995b) found that observers could not discriminate the direction of moving stereoscopic stimuli without trackable features. However, Carney (1997) showed that the use of a brief exposure duration in that study likely produced impaired performance. Recall that Harris and Watamaniuk (1995, 1996) reported that speed discrimination of stereoscopic motion was poor. However, Regan and colleagues (Portfors-Yeomans & Regan, 1996; Kohly & Regan, 1999) provided evidence suggesting that performance was impaired in the Harris and Watamaniuk studies because the stimulus was too small or because the stimulus momentarily disappeared during its trajectory (i.e. as it went across the horopter).

Other studies have provided evidence that stereoscopic motion is likely computed by a low-level motion-sensing mechanism. For example, a number of studies (Patterson et al., 1992; Johns, Rogers & Eagle, 1996; Portfors-Yeomans & Regan, 1996; Donnelly, Bowd & Patterson, 1997; Patterson, Donnelly, Phinney, Nawrot, Whiting & Eyle, 1997; Portfors & Regan, 1997) found that direction and speed of stereoscopic motion was discriminated in complex motion displays that camouflaged or controlled for position information. Smith and Scott-Samuel (1998) showed that stereoscopic motion was perceived in the direction of 'cyclopean motion energy', and not in the direction of trackable features, when a stereoscopic pseudo-squarewave was laterally displaced. These studies eliminated position tracking as a necessary mechanism of stereoscopic motion processing.

Moreover, Bowd, Rose, Phinney and Patterson (1996) found that adaptation to bi-directional stereoscopic motion induced motion aftereffects confined to specific regions of the visual field, suggesting that the stereoscopic motion was computed by retinotopic mechanisms. Adaptation to stereoscopic motion induced direction-selective motion-repulsion aftereffects (Patterson & Becker, 1996) and threshold-elevation aftereffects (Phinney, Bowd & Patterson, 1997), suggesting that the stereoscopic motion was computed by directionally-selective mechanisms. Bowd, Donnelly and Patterson (1997) and Patterson, Bowd and Donnelly (1998) showed that plaid motion and the barber-pole illusion, respectively, were perceived with stereoscopic motion, suggesting that stereoscopic motion signals were used in the representation of moving two-dimensional surfaces. Together, these studies suggested that stereoscopic motion was computed by low-level special-purpose mechanisms located early in the motion stream (for review, see Patterson, 1999)[1].

That stereoscopic motion may be computed early in the motion stream raises the possibility that stereoscopic motion signals are computed by oriented spatial frequency-selective mechanisms, or channels, as posited for luminance motion. Adelson and Bergen (1985) proposed that luminance motion processing involved the filtering of oriented spatial and temporal frequency, with the outputs of quadrature pairs (i.e. 90° out of phase) of spatial and temporal filters being squared and summed to quantify luminance motion energy. A similar computational scheme was proposed by Reichardt (1961), van Santen and Sperling (1984, 1985) and Watson and Ahumada (1983).

Recently, Bex, Verstraten and Mareschal (1996) (see also Over, Broerse, Crassini & Lovegrove, 1973; Cameron, Baker & Boulton, 1992; Ashida & Osaka, 1995; Mareschal, Ashida, Bex, Nishida & Verstraten, 1997) investigated the selectivity of the luminance motion aftereffect for spatial and temporal frequency. These authors varied the relative spatial and temporal frequency between adapt and test stimuli and found that the aftereffect was longest when spatial frequency of adapt and test were equal and temporal frequency of the test was low. Bex et al. (1996) concluded that the luminance motion aftereffect is mediated by a low-pass temporal frequency mechanism and a series of band-pass spatial frequency mechanisms.

Given that stereoscopic motion may be computed early in the motion stream similar to luminance motion, and given that luminance motion is computed by early spatial- and temporal-frequency mechanisms, it is possible that stereoscopic motion is computed by spatial- and temporal-frequency mechanisms that pool

[1] Watamaniuk and McKee (1995) showed that the detection of a trajectory that moved virtually behind occluders was disturbed by motion in the occluders to an equal extent whether the occluders were at the same or different disparity, suggesting that disparity was processed after luminance motion was processed. Stereoscopic motion processing may not be as low-level or early as luminance motion processing.

disparity information at different spatial and temporal scales. Consistent with this idea, there is evidence for the existence of mechanisms selective for stereoscopic (cyclopean) spatial frequency (Tyler, 1974; Schumer & Ganz, 1979; Cobo-Lewis & Yeh, 1994).

The question arises as to whether such stereoscopic spatial-frequency mechanisms play any role in stereoscopic motion processing. To address this question, two experiments investigating the stereoscopic motion aftereffect were performed. *Experiment 1* investigated the spatial-frequency selectivity of the stereoscopic motion aftereffect. Observers adapted to a moving stereoscopic grating of a given spatial frequency of disparity modulation and tested for the aftereffect with a stereoscopic test grating of the same or different spatial frequency. Robust motion aftereffects were induced only when adapt and test spatial frequency was the same. Thus, the stereoscopic motion aftereffect was spatial-frequency selective. *Experiment 2* examined orientation selectivity of the stereoscopic motion aftereffect. Observers adapted to a moving stereoscopic grating of a given orientation of disparity modulation and tested for the aftereffect with a stereoscopic grating of the same or different orientation. Robust motion aftereffects were induced only when adapt and test orientation was the same. Therefore, the stereoscopic motion aftereffect was orientation selective. Given that the stereoscopic motion aftereffect was selective for both spatial frequency and orientation, we concluded that oriented spatial-frequency mechanisms (disparity domain) operated in stereoscopic motion processing.

2. General methods

2.1. Observers

Eight observers served in one or both experiments, five of whom were naive to the purpose of this study. All observers had normal or corrected-to-normal visual acuity and normal binocular vision (tested with a Bausch and Lomb Ortho-Rater and dynamic random-dot stereograms).

2.2. Stimuli

The stimuli were moving grating patterns defined by differences in binocular disparity embedded in dynamic random-dot stereograms (Julesz, 1971). These stereoscopic gratings appeared as square waves that varied in depth (alternating half-cycles were in different depth planes). Half of the bars of the grating had a disparity of 5.7 arcmin crossed from the display screen, and the other bars of the grating had zero disparity (average disparity of the grating = 2.85 arcmin).[2]

To minimize tracking eye movements during adaptation, each adaptation grating was split in half cross-sectionally and presented as two separate panels. The spatial frequency of the half-gratings in the two panels was the same on each trial. A thin strip of background dots (1.44 arcmin wide) containing a fixation point (0.72 square deg) separated the two panels. One panel contained a half-grating moving in one direction and the other panel contained a half-grating moving in the opposite direction at the same speed and temporal frequency (i.e. observers adapted to bidirectional stereoscopic motion). The direction of motion of the two half-gratings alternated across trials. The test grating was also presented as two separate panels each containing a stationary half-grating.

2.3. Apparatus

Stereoscopic stimuli were created with the use of a dynamic random-dot stereogram generation system (Shetty, Brodersen, & Fox, 1979). The display was a 19 in. Barco Chromatics color monitor (refresh rate = 60 Hz; overall display luminance with 50% dot density = 25.2 cd m^{-2}) upon which matrices of red and green random dots were displayed (approximately 5000 dots per matrix). At a viewing distance of 150 cm, the display subtended $14.06 \times 10.64°$. Observers wore glasses that contained red (Wratten No. 29) and green (Wratten No. 58) chromatic filters which segregated the information presented to the two eyes. The mean luminance of the red half-image through the red filter was 2.27 cd m^{-2} while the mean luminance of the green half-image through the green filter was 3.90 cd m^{-2}.

To display the red and green dot matrices, a stereogram generator (hard-wired device) controlled the red and green guns of the Barco monitor. The stereogram generator produced disparity between the two dot arrays by laterally shifting a subset of red dots in one eye's view while leaving unshifted corresponding green dots in the other eye's view.

The gap created by the shift was filled with randomly-positioned dots of the same density and bright-

[2] Square waves defined in the luminance domain could be problematic for examining the spatial-frequency selectivity of the luminance motion aftereffect due to the presence of higher harmonics in the stimulus that might dilute the effects of spatial frequency. However, stereoscopic square-waves defined in the disparity domain would not be as problematic because spatial resolution is very poor in the disparity domain (e.g. Tyler, 1974) and the disparity-defined higher harmonics would not be passed by the cyclopean visual system. We used disparity-defined square-waves because we could not technically generate disparity-defined sine-waves.

ness so that no monocular cues were visible (see below). The observer perceived the shifted subset of dots (which corresponded to half-cycles of the stereoscopic grating) as a stereoscopic form standing out in depth in front of the background dots of the display screen. All dots were replaced dynamically at a rate of 60 Hz, which allowed the stimulus to be moved without monocular cues.[3] The duration of the stimulus was controlled electronically in integer-multiples of the frame duration of the display (16.7 ms).

Signals from a black and white video camera provided input to the stereogram generator, which determined where disparity was inserted in the stereogram. The camera scanned black and white square-wave gratings displayed on a 14 in. computer monitor (Applecolor RGB) and every place the camera encountered a white bar of the grating the camera signaled the stereogram generator to introduce disparity at that place in the stereogram. The scan rate of the computer monitor was synchronized with the scan rate of the camera and the stereogram generator with the use of a RasterOps video card. The moving black and white grating patterns on the computer monitor were created from custom software written in Pascal and run on an Apple IIci computer.

Monocular control trials were performed in which three observers wore either red or green filters over both eyes and made forced-choice direction discrimination judgments for moving stereoscopic gratings. In all cases, the observer never saw the gratings and performance was at chance level. The observers also wore red or green filters over both eyes and adapted to stereoscopic motion. In all cases, the observer never perceived a moving stimulus nor an aftereffect. These results indicate that monocular cues were not visible in our display.

2.4. General procedure

On each trial, the observer adapted for 3 min to a stereoscopic grating moving bidirectionally at a constant speed of 4.68 deg s^{-1} (3 min of adaptation was sufficient to induce stereoscopic motion aftereffects; see Patterson, Bowd, Phinney, Pohndorf, Barton-Howard & Angilletta, 1994; Bowd et al., 1996)[4]. Following adaptation, the observer immediately viewed a stationary test grating and recorded the duration of the aftereffect by depressing the space bar on the computer keyboard. Intertrial interval was 2 min, a duration long enough to allow the aftereffect to dissipate. Five trials were collected under each condition for each observer.

3. Experiment 1

Experiment 1 investigated whether the stereoscopic motion aftereffect was selective for cyclopean spatial frequency. For baseline conditions, the spatial frequency of adapt and test gratings was the same, while for other conditions, the spatial frequency of adapt and test gratings was different. Five spatial frequencies were selected for adaptation: 0.1, 0.2, 0.4, 0.8, and 1.6 cyc deg^{-1}. Three spatial frequencies were selected for test: 0.2, 0.4, and 0.8 cyc deg^{-1}. All gratings were oriented vertically and motion of the gratings was horizontal (i.e. upper half of the grating moved in one direction, leftward or rightward, and lower half of the grating moved in the opposite direction). Six observers participated.

3.1. Results

Aftereffect durations for the five trials collected under each condition were averaged together for each observer and then across observers to provide a single estimate of aftereffect duration for each condition. Fig. 1 shows aftereffect duration for the five adapt and three test spatial frequencies. The maximum aftereffect occurred when adapt and test spatial frequency was the same, and the aftereffect declined as adapt and test spatial frequency became increasingly different.

These data were analyzed by an analysis of variance (ANOVA). The ANOVA showed that there was a significant main effect of adapt spatial frequency [$F(4,20) = 7.65$, $P < 0.001$] but not of test spatial fre-

[3] We performed a control experiment (with three observers from Experiment 2) in which three types of test pattern were compared: (1) static stereo grating and dynamic luminance dots (as in Experiments 1 and 2); (2) dynamic luminance dots only; (3) static stereo grating and static luminance dots. Speed of stereoscopic motion adaptation was 3.69 deg s^{-1}; for conditions 1 and 3, spatial frequency and orientation of the stereo test grating equalled that of the adapting grating, 0.5 cyc deg^{-1} and vertical. The mean duration of the motion aftereffect was 4.0 s for condition 1, but 0 s for conditions 2 and 3. Thus, a grating pattern and dynamic display were necessary for inducing a stereoscopic motion aftereffect (see Nishida & Sato, 1995).

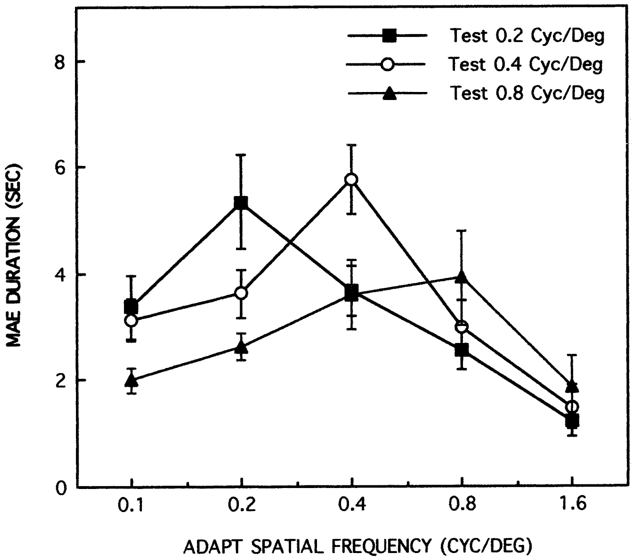

Fig. 1. Duration of the stereoscopic motion aftereffect for five different adapt spatial frequencies (shown on the abscissa) and three test spatial frequencies (given in the legend). Each data point represents an average of six observers. Error bars equal 1 standard error of the mean.

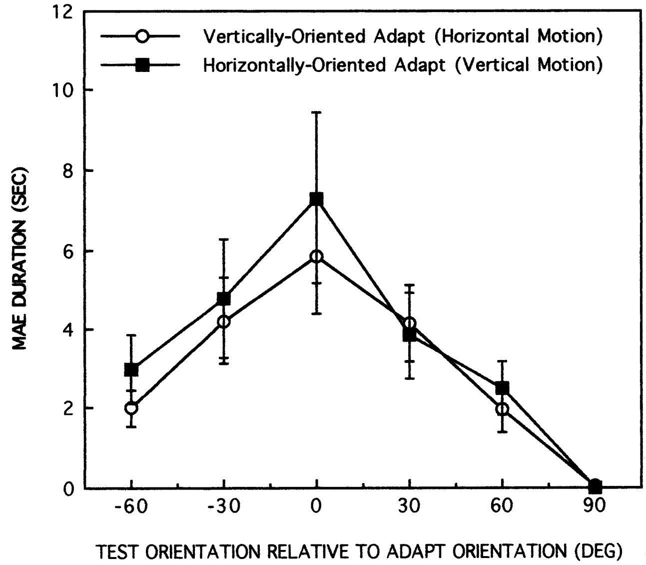

Fig. 2. Duration of the stereoscopic motion aftereffect for six test orientations (shown on the abscissa) normalized relative to two adapt orientations (given in the legend). Positive values on the abscissa indicate clockwise rotations, while negative values indicate counterclockwise rotations, relative to the adapt orientation. Each data point represents an average of five observers. Error bars equal 1 standard error of the mean.

quency [$F(2,10) = 1.13$, $P > 0.05$]. The analysis also showed that adapt spatial frequency and test spatial frequency significantly interacted [$F(8,40) = 3.02$, $P < 0.01$].

These results show that the stereoscopic motion aftereffect was selective for cyclopean spatial frequency.

4. Experiment 2

Experiment 2 investigated whether the stereoscopic motion aftereffect was selective for orientation. For baseline conditions, orientation of adapt and test gratings was the same, while for other conditions, orientation of the adapt and test gratings was different. Two orientations were selected for adaptation: vertically-oriented adapting grating with horizontal adapting motion (i.e. upper half of the grating moved in one direction, leftward or rightward, and the lower half of the grating moved in the opposite direction), and horizontally-oriented adapting grating with vertical adapting motion (i.e. left half of the grating moved in one direction, upward or downward, and the right half of the grating moved in the opposite direction). Relative to a fixed orientation for the adapting grating (vertical or horizontal), six orientations were selected for test: 0° rotation from adapt orientation (baseline); 30, 60, and 90° clockwise rotations from adapt orientation; and 30 and 60° counterclockwise rotations from adapt orientation. Test orientation was varied around a fixed adapting orientation in order to make the direction of adapting motion constant across a given set of conditions. The spatial frequency of the adapt and test gratings was 0.4 cyc deg^{-1}. Five observers participated.

4.1. Results

Aftereffect duration for the five trials collected under each condition for each observer were averaged together as in Experiment 1. Fig. 2 shows aftereffect duration for the two adapt orientations and the six normalized test orientations. The maximum aftereffect occurred when adapt and test orientation was the same, and the aftereffect declined as adapt and test orientation became increasingly different.

These data were analyzed by an ANOVA. The analysis revealed that there was a significant main effect of test orientation [$F(5,20) = 11.85$, $P < 0.001$]. There was no significant main effect of adapt orientation [$F(1,4) = 0.87$, $P > 0.05$] nor any significant interaction between adapt and test orientation [$F(5,20) = 2.14$, $P > 0.05$].

These results show that the stereoscopic motion aftereffect was selective for cyclopean orientation.

5. General discussion

Experiment 1 showed that the stereoscopic motion aftereffect is selective for stereoscopic spatial frequency. Experiment 2 revealed that the stereoscopic motion aftereffect is selective for stereoscopic orientation. Together, these results suggest that the stereoscopic motion aftereffect is produced by adaptation of (cyclopean) oriented band-pass spatial-frequency mechanisms that pool disparity information at different spatial scales and orientations.

These results provide new information about the stereoscopic motion aftereffect (for review, see Moulden, Patterson & Swanston, 1998). Some studies (e.g. Papert, 1964; Anstis, 1980; Braddick, 1980; Zeevi & Geri, 1985; Cavanagh, 1995) found that adaptation to stereoscopic motion did not induce motion aftereffects. Part of the reason for this failure was that these studies employed conditions poorly suited for revealing stereoscopic motion adaptation (e.g. brief adaptation duration). Recent studies reported that adaptation to stereoscopic motion induced robust aftereffects under appropriate conditions.

For example, Patterson et al. (1994) found that induction of the stereoscopic motion aftereffect required a long adaptation duration (greater than 30 s). Patterson et al. also found that the motion aftereffect transferred between the stereoscopic and luminance domains, suggesting that stereoscopic and luminance motion were processed by a common substrate. Nishida and Sato (1995) showed that induction of the stereoscopic motion aftereffect may require dynamic test displays, suggesting that the stereoscopic motion system may be fully engaged only with dynamic stimuli. Patterson, Bowd, Phinney, Lehmkuhle and Fox (1996) found that the stereoscopic motion aftereffect was selective for disparity, suggesting that cells coding for direction of stereoscopic motion also code for disparity. Bowd et al. (1996) found that adapting to bidirectional stereoscopic motion induced bidirectional motion aftereffects (i.e. aftereffects specific to different regions of the visual field), suggesting that the mechanisms mediating the stereoscopic motion aftereffect were retinotopic.

The present study adds to this list of properties by showing that the stereoscopic motion aftereffect is likely to be mediated by the adaptation of spatial-frequency mechanisms, analogous to the luminance motion aftereffect (Ashida & Osaka, 1995; Bex et al., 1996; Cameron et al., 1992; Over et al., 1973; Mareschal et al., 1997). This idea was supported by Smith and Scott-Samuel (1998), who showed that stereoscopic motion was perceived in the direction of 'cyclopean motion energy', and not in the direction of trackable features, when a stereoscopic pseudo-squarewave was laterally displaced. Given that the computation of cyclopean motion energy would require the computation of cyclopean spatial and temporal frequency (see Adelson & Bergen, 1985), the results of Smith and Scott-Samuel also suggested the existence of cyclopean spatial filtering in the visual processing of stereoscopic motion.

The present results are consistent with other research suggesting that stereoscopic motion is likely to be processed by mechanisms that function like early low-level motion sensors. For example, stereoscopic motion is perceived under conditions that eliminated or controlled for position cues and attentional tracking (Patterson et al., 1992; Johns et al., 1996; Carney, 1997; Donnelly et al., 1997; Patterson et al., 1997; Portfors-Yeomans & Regan, 1996); adaptation to stereoscopic motion induces retinotopic aftereffects (Bowd et al., 1996) and directionally-selective aftereffects (Patterson & Becker, 1996; Phinney et al., 1997); stereoscopic motion processing involves the computation of cyclopean motion energy (Smith & Scott-Samuel, 1998); and stereoscopic motion signals appear to be used in the representation of moving two-dimensional surfaces (Bowd et al., 1997; Bowd, Shorter, Becker & Patterson, 1998; Patterson, Bowd, & Donnelly, 1998).

That the stereoscopic motion aftereffect is selective for spatial frequency and orientation indicates that the stereoscopic motion aftereffect involves adaptation of cyclopean oriented spatial-frequency mechanisms. This, in turn, suggests that stereoscopic motion is sensed by early low-level mechanisms (Patterson, 1999) because oriented spatial filtering is thought to be a property of early motion sensing (van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985; Watson & Ahumada, 1983).

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